

# How large should whales be?

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The observed body masses for all extant cetacean species, including the 175,000,000 g Blue Whale, are predicted, with no tunable parameters, by a macroevolutionary tradeoff between short-term selective advantages and long-term extinction risks from increased species body size, unfolding in a pelagic environment. Dramatic size differences between terrestrial and aquatic mammals are thus the result of increased convective heat loss in water, which induces a minimum viable size orders of magnitude larger than the 2 g limit induced by air for terrestrial mammals. The large minimum size would have presented a high macroevolutionary barrier to mammals becoming fully aquatic and explains the historical timing of mammals' invasion of aquatic habits.

Keywords: body mass distribution, cetaceans, macroevolution, cladogenesis

Cetaceans include the largest animals ever to live, including the Blue Whale (*Balaenoptera musculus*), which is nearly 30 times larger than an African elephant and twice as large as the largest sauropod. However, the evolutionary and ecological reasons for their enormous sizes or the possibility of still larger animals remains unclear. A deeper understanding of the mechanisms shaping cetacean sizes would shed light on the interaction of macroecological [7] and macroevolutionary processes [44], on long-term trends in species mass [3, 4], e.g., Cope's rule, the empirically observed tendency for species masses to increase within a lineage over evolutionary time [2, 43], and may inform conservation efforts.

Many major animal clades, including mammals, birds, fish and insects, seem to exhibit a canonical pattern in the distribution of species masses [1, 10, 24, 43]. For example, the most common size of a terrestrial mammal is roughly 40 g (common Pacific Rat, *Rattus exulans*). Both larger and smaller species are much less common, but asymmetrically so: the largest species, like the extinct Imperial Mammoth (*Mammuthus imperator*,  $10^7$  g), are orders of magnitude larger, while the smallest, like Remy's Pygmy Shrew (*Suncus remyi*, 2 g), are only a little smaller (Fig. 1).

Both the precise shape and the origins of its ubiquity have long been a topic of ecological interest. Recently, this characteristic pattern was shown to be a long-term consequence when a minimum viable body size, e.g., from physiological or thermoregulatory limits, constrains a tradeoff between short-term selective advantages [7] and long-term extinction risks from increased species size [10, 11] (Fig. 2a). Other studies have suggested that the pattern is caused by competition about a taxon-specific energetically optimal body size [8, 26, 39]; however, evidence of Cope's rule—descendant species tend to be larger than their ancestors—and the fact that most species are not close to their group's predicted optimal

size (among other reasons [24]) suggest that this theory may be flawed.

Here, we consider the body masses of cetaceans, which also exhibit the canonical right-skewed pattern (Fig. 1): the median size (356 kg, *Tursiops truncatus*) is close to the smallest (37.5 kg, *Pontoporia blainvillei*) but far from the largest (175,000 kg). This fact is notable because Cetacea is a modest-sized clade (77 extant species) within Mammalia and claims about canonical size distributions have primarily been made about much more speciose and higher-level taxonomic groupings. Furthermore, Cetacea is the largest and most diverse aquatic mammal clade (Sirenia has only five extant species). Cetacean sizes thus provide a unique test of the macroevolutionary tradeoff hypothesis. They allow us to test whether the same short-term-long-term tradeoff that explains the sizes of terrestrial mammals also explain the sizes of whales, and to investigate the impact of an aquatic environment on mammalian body size evolution.

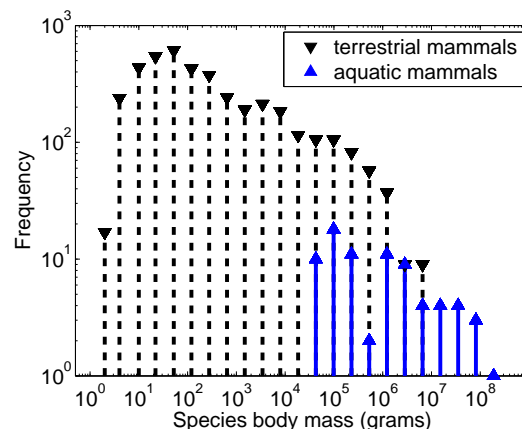


FIG. 1: Terrestrial (includes semi-aquatic) [40] and fully aquatic mammal species mass distributions. Both show the canonical asymmetric pattern: the median size is flanked by a short left-tail down to a minimum viable size and a long right-tail out to a few extremely large species.

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We show that the tradeoff mechanism is universal for mammals. Using a cladogenetic diffusion model estimated from fossil and extant terrestrial mammal data, but with a minimum viable size appropriate for aquatic endotherms, we produce a statistically accurate, zero-parameter prediction of extant cetacean masses. This strong agreement implies that a single macroevolutionary tradeoff explains both aquatic and terrestrial mammal sizes. We close with a brief discussion of the ecological and evolutionary theoretical implications.

## I. NEUTRAL MODEL FOR CETACEAN SIZES

Following Clauset and Erwin [10], we model the trade-off hypothesis as constrained cladogenetic diffusion.

First, a species of mass  $M$  produces descendant species with masses  $\lambda M$  (Fig. 2b), where  $\lambda$  is a random variable representing short-term selective effects on size [29, 43]. With each  $\lambda$  drawn independently, short-term selections on body sizes are uncorrelated across the clade and the clade's size distribution evolves according to a diffusion process. The trajectory of any particular lineage follows a kind of random walk. When the average size change between ancestors and descendants within a lineage is biased toward larger sizes (Cope's rule), we have  $\langle \ln \lambda \rangle > 0$  [2]. (Size variation between speciation events need not be modeled separately because its impact may be absorbed into  $\lambda$ .)

Second, species may not take any size and thus the diffusion process is constrained. On the upper end, the probability of species extinction rises gently with increasing size [25], e.g., due to larger energetic requirements, smaller species abundance and longer generational times. The net effect is a soft upper limit. Given a particular extinction risk curve, the number and size of very large species is determined by the total number of species in the clade, which sets the rate at which smaller-sized lineages migrate into the larger and more risky size ranges [48].

On the lower end, endothermy imposes a minimum viable mass—a hard lower limit—that prohibits evolution toward ever smaller sizes. For terrestrial mammals and birds, this thermoregulatory minimum size is known to occur at  $M_{\min} = 2$  g [33, 50], below which a species' convective heat loss in air is too high to maintain its internal temperature.

To extract precise predictions for the distribution of species sizes, we formalize this model mathematically. Following Clauset and Redner [11],  $c(x, t)$  denotes the density (fraction) of species having mass  $x = \ln M$  at time  $t$ . Under mild assumptions, the value  $c(x, t)$  obeys the convection-diffusion-reaction equation in the continuum limit:

$$\frac{\partial c}{\partial t} + v \frac{\partial c}{\partial x} = D \frac{\partial^2 c}{\partial x^2} + (k - A - Bx)c, \quad (1)$$

where  $v = \langle \ln \lambda \rangle$  is the bias or average change in size from ancestor to descendent,  $D = \langle (\ln \lambda)^2 \rangle$  is the diffusion

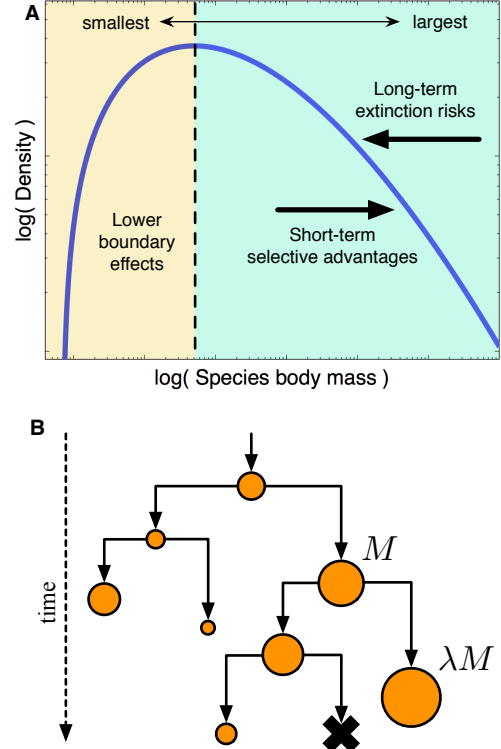


FIG. 2: (A) The characteristic distribution of species body sizes, observed in most major animal groups. Macroevolutionary tradeoffs between short-term selective advantages and long-term extinction risks, constrained by a minimum viable size  $M_{\min}$ , produce the distribution's long right-tail. (B) Schematic illustrating the cladogenetic diffusion model of species body-size evolution: a descendant species' mass is related to its ancestor's size  $M$  by a random multiplicative factor  $\lambda$ . Species become extinct with a probability that grows slowly with  $M$ .

coefficient or the variance in size change, and  $k - A$  is the size-independent (background) net speciation rate, which sets the absolute scale of the mass frequencies.

The aforementioned size constraints ensure convergence on a steady state distribution. To solve for its shape, we change variables  $\mu = v/D$ ,  $\alpha = (k - A)/D$ , and  $\beta = B/D$ , and require that the distribution go to zero at  $x = x_{\min}$ . It can then be shown that the steady-state distribution of sizes  $x$  is

$$c(x) \propto e^{\mu x/2} \text{Ai} \left[ \beta^{1/3} (x - x_{\min}) + z_0 \right], \quad (2)$$

where  $\text{Ai}[\cdot]$  is the Airy function and  $z_0 = -2.3381 \dots$  is the location of its first zero [11, 12].

In this way, the predicted shape of the species size distribution is fully determined by three model parameters:  $\mu$ , the normalized strength of Cope's rule,  $\beta$ , the normalized size-dependence of extinction risk, and  $x_{\min}$ , the logarithm of the minimum viable body size.

Estimates for  $\mu$  and  $\beta$  for terrestrial mammals have previously been derived from fossil and extant data. The resulting size distribution accurately reproduces both the extant sizes of terrestrial mammals [10] and their expansion during the late Cretaceous and early Paleogene [11, 51]. Removing either the size-dependence of extinction risk or the minimum viable size produces unrealistic predictions [10].

However, pelagic environments impose distinct physiological, ecological and evolutionary challenges for endothermic mammals, which are not reflected in the terrestrial model. One critical difference is the greater convective heat loss in water, which raises the minimum size of a competent aquatic endotherm. Thermoregulatory calculations and empirical data both estimate roughly  $M_{\min} = 7 \text{ kg}$  for extant cetaceans [15], about 3500 times larger than the minimum size in air.

## II. TESTS OF THE MODEL PREDICTIONS

To test the tradeoff hypothesis for cetaceans, we use the terrestrial mammal model, but we shift  $M_{\min}$  to its pelagic value. That is, we use a model that successfully explains the sizes of terrestrial mammal species but we change the environmental constraint imposed by  $M_{\min}$  so that the tradeoff unfolds in a pelagic environment. This produces an *ex ante* prediction  $\text{Pr}(M)$  for extant cetacean species sizes. Notably, the prediction has no tunable parameters by which to improve its agreement with observed sizes. This property makes its accuracy a strong test of the tradeoff's universality.

Previous analyses of terrestrial mammal data yielded  $\hat{\mu} \approx 0.2$ , a slight tendency toward larger sizes within a lineage (Cope's rule), and  $\hat{\beta} \approx 0.08$ , a weak tendency for extinction to increase with body size [11, 12].

To test the model's accuracy, we constructed a novel body size data set for all 77 extant cetacean species, from 183 empirical size estimates [5, 6, 9, 13, 14, 16–23, 27, 30–32, 34–38, 40–42, 45–47, 49]. Only plausibly independent, scientifically derived estimates were included. Mass ranges were converted to point estimates by taking their midpoint, unless a mean value was also provided. Subsequently, the mean value of all point estimates for a given species was used; this yielded an average of 2.4 measurements per species. Tables I and II give the mass estimates, primary source(s) and data curation comments.

Figure 3 compares the predicted and empirical distributions. We determined the prediction's statistical plausibility relative to the empirical sizes via a standard two-tailed Kolmogorov-Smirnov test, evaluated numerically. The resultant value  $p_{ks} = 0.16 \pm 0.01$  exceeds all conventional thresholds for rejecting the null hypothesis, indicating that extant cetacean sizes are statistically indistinguishable from the predicted distribution. To simulate statistical uncertainty in  $\mu$  and  $\beta$ , we estimated  $p_{ks}$  via Monte Carlo by adding a small amount of Normally distributed noise to the terrestrial parameter val-

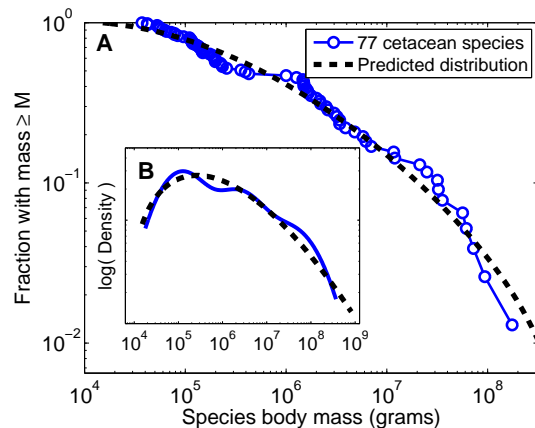


FIG. 3: (A) *Ex ante* predicted cetacean sizes, from a cladogenetic model fitted to terrestrial mammals but with a pelagic  $M_{\min}$  (see text), and empirical sizes of 77 extant cetacean species, as complementary cumulative distributions and as (B) smoothed probability densities.

ues. This yields a slightly lower but still non-significant  $p_{ks} = 0.07 \pm 0.03$ , which does not alter our conclusion. Thus, the macroevolutionary tradeoff fully explains the observed sizes of cetacean species as a group.

As an additional test, we consider whether the size of the largest cetacean species would be considered a statistical outlier. The probability of observing at least one species with size at least as large as the Blue Whale at  $M_* = 1.75 \times 10^8 \text{ g}$  was computed as  $p(M_*) = 1 - F(M_*)^n$  where  $F(M_*) = \int_{M_{\min}}^{M_*} \text{Pr}(M) dM$  is the portion of the predicted distribution below  $M_*$  and  $n$  is the number of iid observations (extant species) drawn from  $\text{Pr}(M)$ . Taking fixed parameters yields  $p = 0.91$ ; simulating statistical uncertainty via Monte Carlo (as above) yields  $p = 0.88 \pm 0.03$ , which is consistent with the fixed-parameter result.

Thus, the enormous size of the Blue Whale is not a statistical outlier relative to the predicted distribution, implying that the tradeoff mechanism alone is sufficient explanation of the Blue Whale's size. We note, however, that a species somewhat larger than the Blue Whale would also not be statistically unlikely, although no such species is known to have existed.

Finally, the value of  $\beta$  used here was estimated by fitting the model to extant terrestrial mammal data. Estimating  $\beta$  directly from the extant cetacean species size distribution only improves the fit of the model and thus cannot change our conclusions. Doing so yields  $\hat{\beta}_{\text{cete}} \approx 0.097$ , which is close to the terrestrial mammals value and supports our universality claim for the underlying processes shaping mammal evolution.

### III. DISCUSSION

The accuracy of the model's *ex ante* prediction confirms that terrestrial and aquatic mammal sizes are shaped by a single macroevolutionary tradeoff between short-term advantages—better resource fluctuation tolerance, thermoregulation and predator avoidance [7]—and long-term extinction risks—larger energetic requirements, smaller species abundance and longer generational times—of increased size, constrained by endothermic requirements at the lower end. Thus, cetaceans exhibit large body sizes because greater convective heat loss in water raises the minimum viable size, which shifts the canonical distribution upward and pushes its tail into size ranges inaccessible to terrestrial mammals.

This large minimum size was a significant barrier for early terrestrial mammals, preventing their invasion of pelagic niches prior to roughly 60 Ma. Before this time, there were few or no mammal species with sufficiently large masses [28], and therefore no mammals capable of living as competent aquatic endotherms. Only after the terrestrial mammal size distribution expanded in the late Cretaceous and early Paleogene [11, 51] was such a transition possible, and mammals successfully invaded the oceans almost immediately after these conditions were met.

The general pattern of extant cetacean body sizes is compactly explained by only the normalized strength of Cope's rule  $\mu$  and the normalized size-dependence of extinction risks  $\beta$ , which take universal values for all mammals, terrestrial and aquatic. Given the first archaeocete's size, species counts over geological time and the model diffusion rate, the model would predict when a species of a given size should first have appeared.

The success of the constrained cladogenetic diffusion model and the tradeoff hypothesis in predicting, without tunable parameters, the sizes of extant cetaceans further

suggests that the energetically optimal body size explanation of the species size distribution is flawed. This, in turn, suggests that the empirically observed pattern of size changes among insular species [26, 39], and their hypothesized explanation [8], should be revisited.

The short-term-long-term tradeoff dynamic described here is a neutral mechanism for species size evolution within a clade, as it omits explicit mechanisms for ecologically important processes like species interaction, geography, climate, etc. Deviations from the predictions, like the slight over-abundance of cetaceans near 800 kg and under-abundance near 100,000 kg (Fig. 3a), may indicate previously unrecognized non-neutral evolutionary or ecological processes. Similarly, to the extent that they can be measured in empirical data, changes in model parameter values over time may indicate broad-scale, non-stationary processes like climate change, e.g., in the value on  $x_{\min}$  or the magnitude of  $\mu$ , or clade-level ecological competition, as between mammals and dinosaurs prior to the K-Pg event.

Finally, our assumptions of size-related macroevolutionary tradeoffs are entirely general, but it remains unknown whether they hold for other major clades, including aquatic tetrapod groups like ichthyosaurs, plesiosaurs and turtles, or dinosaurs, fish and foraminifera, or whether it holds for other small taxonomic groups. A broad examination of minimum viable sizes and size-dependent extinction risks across groups and across geologic time may better elucidate the role of species size in major evolutionary transitions and ecological theory.

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group	family	species	mass (kg)	primary source (reference)	curation comments
Mysticeti	Balaenidae	Balaena mysticetus	100000	Smith etal (2003)	.
Mysticeti	Balaenidae	Balaena mysticetus	87500	Jefferson Leatherwood Webber (1993)	.
Mysticeti	Balaenidae	Eubalaena australis	23000	Smith etal (2003)	.
Mysticeti	Balaenidae	Eubalaena australis	100000	Jefferson Leatherwood Webber (1993)	.
Mysticeti	Balaenidae	Eubalaena glacialis	23000	Smith etal (2003)	.
Mysticeti	Balaenidae	Eubalaena glacialis	90000	Jefferson Leatherwood Webber (1993)	.
Mysticeti	Balaenopteridae	Balaenoptera acutorostrata	10000	Smith etal (2003)	.
Mysticeti	Balaenopteridae	Balaenoptera acutorostrata	14000	Jefferson Leatherwood Webber (1993), Perrin Zubitsova Kuzmin (2004)	.
Mysticeti	Balaenopteridae	Balaenoptera borealis	20000	Smith etal (2003)	.
Mysticeti	Balaenopteridae	Balaenoptera borealis	30000	Jefferson Leatherwood Webber (1993), Long 1968	.
Mysticeti	Balaenopteridae	Balaenoptera edeni	20000	Smith etal (2003)	.
Mysticeti	Balaenopteridae	Balaenoptera edeni	22500	Jefferson Leatherwood Webber (1993)	.
Mysticeti	Balaenopteridae	Balaenoptera musculus	190000	Smith etal (2003)	.
Mysticeti	Balaenopteridae	Balaenoptera musculus	160000	Jefferson Leatherwood Webber (1993), Morton ed 1997	.
Mysticeti	Balaenopteridae	Balaenoptera physalus	70000	Smith etal (2003)	.
Mysticeti	Balaenopteridae	Balaenoptera physalus	75000	Jefferson Leatherwood Webber (1993), Uhen Fordyce Barnes 1998 inJanisGunnellUhen	.
Mysticeti	Balaenopteridae	Megaptera novaeangliae	30000	Smith etal (2003)	.
Mysticeti	Balaenopteridae	Megaptera novaeangliae	35000	Jefferson Leatherwood Webber (1993), Clapham Mead 1999, Uhen Fordyce Barnes 1998 inJanisGunnellUhen	.
Mysticeti	Eschrichtiidae	Eschrichtius robustus	28500	Smith etal (2003)	.
Mysticeti	Eschrichtiidae	Eschrichtius robustus	35000	Jefferson Leatherwood Webber (1993), Uhen Fordyce Barnes 1998 inJanisGunnellUhen	.
Mysticeti	Neobalaenidae	Caperea marginata	3200	Jefferson Leatherwood Webber (1993), Perrin Zubitsova Kuzmin (2004)	estimate by Smith etal 2003 gives a mass 10x as large, so we omit Smith etal
Odontoceti	Delphinidae	Cephalorhynchus commersonii	72.4	Smith etal (2003)	.
Odontoceti	Delphinidae	Cephalorhynchus commersonii	76	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Cephalorhynchus commersonii	86	Culik (2004)	.
Odontoceti	Delphinidae	Cephalorhynchus eutropia	45	Smith etal (2003)	.
Odontoceti	Delphinidae	Cephalorhynchus eutropia	63	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Cephalorhynchus eutropia	60	Culik (2004)	.
Odontoceti	Delphinidae	Cephalorhynchus heavisidii	40	Smith etal (2003)	.
Odontoceti	Delphinidae	Cephalorhynchus heavisidii	65	Culik (2004)	.
Odontoceti	Delphinidae	Cephalorhynchus hectori	50	Smith etal (2003)	.
Odontoceti	Delphinidae	Cephalorhynchus hectori	57	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Delphinus delphis	80	Smith etal (2003)	.
Odontoceti	Delphinidae	Delphinus delphis	135	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Delphinus delphis	200	Culik (2004)	.
Odontoceti	Delphinidae	Feresa attenuata	170	Smith etal (2003)	.
Odontoceti	Delphinidae	Feresa attenuata	225	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Globicephala macrorhynchus	726	Smith etal (2003)	.
Odontoceti	Delphinidae	Globicephala macrorhynchus	3600	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Globicephala melas	800	Smith etal (2003)	.
Odontoceti	Delphinidae	Globicephala melas	2000	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Globicephala melas	1600	Perrin Zubitsova Kuzmin (2004)	.
Odontoceti	Delphinidae	Grampus griseus	387.5	Smith etal (2003)	.
Odontoceti	Delphinidae	Grampus griseus	400	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lagenodelphis hosei	164	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenodelphis hosei	210	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lagenodelphis hosei	210	Culik (2004)	.
Odontoceti	Delphinidae	Lagenodelphis hosei	209	Jefferson Leatherwood 1994	.
Odontoceti	Delphinidae	Lagenorhynchus acutus	182	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenorhynchus acutus	208.5	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lagenorhynchus acutus	205	Culik (2004)	.
Odontoceti	Delphinidae	Lagenorhynchus albirostris	180	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenorhynchus albirostris	265	Culik (2004)	.
Odontoceti	Delphinidae	Lagenorhynchus australis	120	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenorhynchus australis	115	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lagenorhynchus australis	115	Culik (2004)	.
Odontoceti	Delphinidae	Lagenorhynchus cruciger	110	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenorhynchus obliquidens	120	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenorhynchus obliquidens	180	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lagenorhynchus obliquidens	82.5	Culik (2004)	.
Odontoceti	Delphinidae	Lagenorhynchus obscurus	127.5	Smith etal (2003)	.
Odontoceti	Delphinidae	Lagenorhynchus obscurus	60	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lagenorhynchus obscurus	100	Culik (2004)	.
Odontoceti	Delphinidae	Lissodelphis borealis	113	Smith etal (2003)	.
Odontoceti	Delphinidae	Lissodelphis borealis	115	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Lissodelphis borealis	116	Culik (2004)	.
Odontoceti	Delphinidae	Lissodelphis borealis	113	Jefferson Newcomer (1993)	.
Odontoceti	Delphinidae	Lissodelphis peronii	116	Smith etal (2003)	.
Odontoceti	Delphinidae	Lissodelphis peronii	116	Jefferson Leatherwood Webber (1993)	Culik 2004 repeats this measurement, so we omit Culik
Odontoceti	Delphinidae	Lissodelphis peronii	116	Newcomer Jefferson Brownell 1996	.
Odontoceti	Delphinidae	Orcaella brevirostris	190	Smith etal (2003)	.
Odontoceti	Delphinidae	Orcaella brevirostris	122.5	Culik (2004)	.
Odontoceti	Delphinidae	Orcaella brevirostris	123.5	Stacey Arnold 1999	.
Odontoceti	Delphinidae	Orcinus orca	4300	Smith etal (2003)	.
Odontoceti	Delphinidae	Orcinus orca	8750	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Orcinus orca	4685	Culik (2004)	.
Odontoceti	Delphinidae	Orcinus orca	7050	Perrin Zubitsova Kuzmin (2004)	reported mass mean of 2 specimens
Odontoceti	Delphinidae	Peponocephala electra	208	Smith etal (2003)	.
Odontoceti	Delphinidae	Peponocephala electra	275	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Peponocephala electra	228	Culik (2004)	.
Odontoceti	Delphinidae	Peponocephala electra	208	Jefferson Barros 1997	.
Odontoceti	Delphinidae	Pseudorca crassidens	1360	Smith etal (2003)	.
Odontoceti	Delphinidae	Pseudorca crassidens	2000	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Pseudorca crassidens	1360	Stacey Leatherwood 1994	.
Odontoceti	Delphinidae	Sotalia fluviatilis	44	Smith etal (2003)	.
Odontoceti	Delphinidae	Sotalia fluviatilis	40	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Sousa chinensis	265	Smith etal (2003)	.
Odontoceti	Delphinidae	Sousa chinensis	284	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Sousa chinensis	215	Culik (2004)	.
Odontoceti	Delphinidae	Sousa chinensis	265	Jefferson Karczmarksi (2001)	.
Odontoceti	Delphinidae	Sousa teuszii	100	Smith etal (2003)	.
Odontoceti	Delphinidae	Sousa teuszii	284	Jefferson Leatherwood Webber (1993)	.
Odontoceti	Delphinidae	Sousa teuszii	215	Culik (2004)	.
Odontoceti	Delphinidae	Sousa teuszii	166	Waerebeek etal (2004)	.

TABLE I: Cetacean size estimates (part 1).

group	family	species	mass (kg)	primary source (reference)	curation comments
Odontoceti	Delphinidae	Stenella attenuata	120	Jefferson Leatherwood Webber (1993)	estimate from Smith etal 2003 is less than 1/2 of the values reported elsewhere, so we omit Smith etal
Odontoceti	Delphinidae	Stenella attenuata	119	Culik (2004)	
Odontoceti	Delphinidae	Stenella attenuata	119	Perrin (2001)	
Odontoceti	Delphinidae	Stenella clymene	68	Smith etal (2003)	
Odontoceti	Delphinidae	Stenella clymene	85	Jefferson Leatherwood Webber (1993)	
Odontoceti	Delphinidae	Stenella clymene	80	Culik (2004)	
Odontoceti	Delphinidae	Stenella clymene	80	Jefferson Curry (2003)	
Odontoceti	Delphinidae	Stenella coeruleoalba	135.9	Smith etal (2003)	
Odontoceti	Delphinidae	Stenella coeruleoalba	156	Jefferson Leatherwood Webber (1993)	
Odontoceti	Delphinidae	Stenella coeruleoalba	156	Culik (2004)	
Odontoceti	Delphinidae	Stenella frontalis	110	Smith etal (2003)	
Odontoceti	Delphinidae	Stenella frontalis	143	Jefferson Leatherwood Webber (1993)	
Odontoceti	Delphinidae	Stenella frontalis	143	Culik (2004)	
Odontoceti	Delphinidae	Stenella frontalis	140	Perrin (2002)	
Odontoceti	Delphinidae	Stenella longirostris	50.5	Smith etal (2003)	
Odontoceti	Delphinidae	Stenella longirostris	77	Jefferson Leatherwood Webber (1993)	
Odontoceti	Delphinidae	Stenella longirostris	50.5	Perrin 1998	Culik 2004 repeats measurement of Perrin 1998, so we omit Culik
Odontoceti	Delphinidae	Steno bredanensis	130	Smith etal (2003)	
Odontoceti	Delphinidae	Steno bredanensis	150	Jefferson Leatherwood Webber (1993)	
Odontoceti	Delphinidae	Steno bredanensis	155	Culik (2004)	
Odontoceti	Delphinidae	Tursiops truncatus	175	Smith etal (2003)	
Odontoceti	Delphinidae	Tursiops truncatus	650	Jefferson Leatherwood Webber (1993)	
Odontoceti	Delphinidae	Tursiops truncatus	242	Culik (2004)	
Odontoceti	Monodontidae	Delphinapterus leucas	1360	Smith etal (2003)	
Odontoceti	Monodontidae	Delphinapterus leucas	1500	Steward Steward (1989), Uhen Fordyce Barnes 1998	
Odontoceti	Monodontidae	Delphinapterus leucas	1500	inJanisGunnellUhen	
Odontoceti	Monodontidae	Delphinapterus leucas	1600	Culik (2004)	
Odontoceti	Monodontidae	Monodon monoceros	900	Smith etal (2003)	
Odontoceti	Monodontidae	Monodon monoceros	1600	Jefferson Leatherwood Webber (1993), Reeves Tracey (1980)	
Odontoceti	Monodontidae	Monodon monoceros	1300	Culik (2004)	
Odontoceti	Phocoenidae	Australophocaena dioptrica	65	Smith etal (2003)	
Odontoceti	Phocoenidae	Neophocaena phocaenoides	32.5	Smith etal (2003)	
Odontoceti	Phocoenidae	Neophocaena phocaenoides	85	Culik (2004)	
Odontoceti	Phocoenidae	Neophocaena phocaenoides	71.8	Jefferson Hung (2004)	
Odontoceti	Phocoenidae	Phocoena phocoena	52.5	Smith etal (2003)	
Odontoceti	Phocoenidae	Phocoena phocoena	57.5	Jefferson Leatherwood Webber (1993)	
Odontoceti	Phocoenidae	Phocoena phocoena	55	Culik (2004)	
Odontoceti	Phocoenidae	Phocoena sinus	42.5	Smith etal (2003)	
Odontoceti	Phocoenidae	Phocoena spinipinnis	60	Smith etal (2003)	
Odontoceti	Phocoenidae	Phocoena spinipinnis	85	Jefferson Leatherwood Webber (1993)	
Odontoceti	Phocoenidae	Phocoenoides dalli	102.5	Smith etal (2003)	
Odontoceti	Phocoenidae	Phocoenoides dalli	200	Jefferson Leatherwood Webber (1993)	
Odontoceti	Phocoenidae	Phocoenoides dalli	200	Culik (2004)	
Odontoceti	Phocoenidae	Phocoenoides dalli	200	Jefferson (1988)	
Odontoceti	Physeteridae	Kogia breviceps	431.5	Culik (2004), Borsa (2006), Uhen Fordyce Barnes (1998)	
Odontoceti	Physeteridae	Kogia breviceps	450	inJanisGunnellUhen	
Odontoceti	Physeteridae	Kogia breviceps	400	Borsa (2006), Jefferson Leatherwood Webber (1993), Uhen Fordyce Barnes (1998) inJanisGunnellUhen	
Odontoceti	Physeteridae	Kogia simus	183.1	Smith etal (2003)	
Odontoceti	Physeteridae	Kogia simus	270	Nagorsen 1985	
Odontoceti	Physeteridae	Kogia simus	270	Culik (2004)	mass quoted as 2702 kg, but this is too big by an order of magnitude. Assumed to be 270.2kg
Odontoceti	Physeteridae	Kogia simus	210	Jefferson Leatherwood Webber (1993)	
Odontoceti	Physeteridae	Physeter catodon	14025	Smith etal (2003)	
Odontoceti	Physeteridae	Physeter catodon	57000	Jefferson Leatherwood Webber (1993), Cranford (1999)	
Odontoceti	Platanistidae	Inia geoffrensis	129.25	Smith etal (2003)	
Odontoceti	Platanistidae	Inia geoffrensis	160	Jefferson Leatherwood Webber (1993)	
Odontoceti	Platanistidae	Inia geoffrensis	167.5	Culik (2004)	
Odontoceti	Platanistidae	Inia geoffrensis	129.25	Best Silva (1993)	
Odontoceti	Platanistidae	Lipotes vexillifer	187.5	Jefferson Leatherwood Webber (1993)	mass estimate from Smith etal 2003 is less than 1/2 estimated range here, so we omit Smith etal
Odontoceti	Platanistidae	Platanista gangetica	115	Smith etal (2003)	
Odontoceti	Platanistidae	Platanista gangetica	108	Jefferson Leatherwood Webber (1993)	
Odontoceti	Platanistidae	Platanista minor	83.9146	Smith etal (2003)	
Odontoceti	Platanistidae	Pontoporia blainvillei	40.5	Smith etal (2003)	
Odontoceti	Platanistidae	Pontoporia blainvillei	34	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Berardius arnuxii	7000	Smith etal (2003)	
Odontoceti	Ziphiidae	Berardius bairdii	11380	Smith etal (2003)	
Odontoceti	Ziphiidae	Berardius bairdii	12000	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Hyperoodon ampullatus	5800	Smith etal (2003)	
Odontoceti	Ziphiidae	Hyperoodon planifrons	3000	Smith etal (2003)	
Odontoceti	Ziphiidae	Indopacetus pacificus	2200	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon bidens	3400	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon bowdoini	2600	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon carlhubbsi	1400	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Mesoplodon carlhubbsi	3400	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon carlhubbsi	500	Mean Walker Houck 1982	
Odontoceti	Ziphiidae	Mesoplodon densirostris	2300	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon densirostris	1033	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Mesoplodon europaeus	5600	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon europaeus	1200	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Mesoplodon ginkgodens	1500	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon grayi	2900	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon grayi	1100	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Mesoplodon hectori	1000	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon layardii	1500	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon mirus	2100	Smith etal (2003)	
Odontoceti	Ziphiidae	Mesoplodon mirus	1400	Jefferson Leatherwood Webber (1993)	
Odontoceti	Ziphiidae	Mesoplodon mirus	1400	Culik (2004)	
Odontoceti	Ziphiidae	Mesoplodon stejnegeri	4800	Smith etal (2003)	
Odontoceti	Ziphiidae	Tasmacetus shepherdii	2500	Smith etal (2003)	
Odontoceti	Ziphiidae	Ziphius cavirostris	4775	Smith etal (2003)	
Odontoceti	Ziphiidae	Ziphius cavirostris	3000	Jefferson Leatherwood Webber (1993)	

TABLE II: Cetacean size estimates (part 2).